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IN SITU OBSERVATIONS ON THREE SPECIES OF LARGE-FINNED DEEP-SEA SQUIDS

M. Vecchione, C. F. E. Roper, E. A. Widder and T. M. Frank

ABSTRACT

The manned submersible JOHNSON SEA-LINK II was used for a series of dives on the continental slope of the eastern Gulf of Mexico in September 1995. The deep-sea squids *Mastigoteuthis hjorti* Chun, 1913 and *Octopoteuthis megaptera* (Verrill, 1885) were repeatedly observed at depths of 600–850 m. Both species were videotaped alive, in situ, for the first time during these dives. These species share the characteristic of very large fins, almost as long as the mantle length, but their swimming behavior observed in the vicinity of the submersible differed greatly. Throughout most of the videotaped sequences of *O. megaptera*, it swam with its body oriented obliquely with the head upward, arms flexed laterally and dorsally. The fins flapped in the arc between overlapping ventrally and extending laterally, never traversing dorsally above the body plane. Conversely, the near-bottom observations of *M. hjorti* showed it to behave similarly to previous descriptions of *Mastigoteuthis magna*, orienting vertically with the head down and tentacles extended to the sediment. This orientation is maintained by gentle, complex undulation of the fins. A third species with very large fins and extremely long arms was observed near the bottom from an ROV at approximately 2200 m in January 2000. While it differed from any previously known family, it behaved similarly to a mastigoteuthid. We now believe this specimen was a ‘big-fin’, family Magnapinnidae Vecchione and Young, 1998. If so, this observation and a similar squid recently observed and video-taped from a submersible in the Indian Ocean extend the known distribution of the recently discovered family to deep waters in subtropical areas around the globe.

The biology and behavior of deep-sea cephalopods are poorly known. Inferences about functional biology have been based mostly on anatomical structure and comparison with better-known, shallow-living relatives. Such inferences often have proved to be incorrect once direct observations become available (Vecchione, 1997). Thus an assumption that morphological similarity may indicate similarity in function and behavior may not be justified a priori. The use of deep-diving submersibles to photograph and videotape living cephalopods and to capture them in excellent condition has revolutionized our understanding of their behavior and functional morphology during the past decade (e.g., Roper and Vecchione, 1996, 1997; Johnsen et al., 1998, 1999; Vecchione and Roper, 1992; Vecchione and Young, 1997; Young, 1995).

We present direct in situ observations on the behavior of three species of deep-sea squids recorded from submersibles in the Gulf of Mexico. All three share the characteristic of very large fins relative to the size of the mantle and head. Our primary focus is the function of the large fins in swimming, but we include other observations on behavior as well. One of these species does not convincingly match the known characteristics of any described family of cephalopods. We therefore discuss the possible identity of this unusual squid.

MATERIALS AND METHODS

The series of 15 dives using the JOHNSON SEA-LINK II (JSL) manned submersible was conducted mostly during daytime from 16–24 September 1995 in the vicinity of 27°05'N, 85°00'W in the northern Gulf of Mexico. When cephalopods were seen, videotapes were recorded either with an external camera, in which case they became part of the logged dive, or with a small handheld video camera operated by the scientist in the transparent sphere, in which case detailed data on depth, temperature, etc. may not have been recorded.

Additionally, a remotely operated vehicle (ROV) operated from the commercial oil-drilling ship MILLENNIUM EXPLORER of R & B Falcon Co. videotaped an unusual squid with huge fins and long, tendrilous arms in the Mississippi Canyon, Gulf of Mexico (approximately 28°37'N, 88°00'W) at 7,196 ft (2195 m) depth on 25 January 2000 (1149 hrs).

OBSERVATIONS

Mastigoteuthis hjorti Chun, 1913

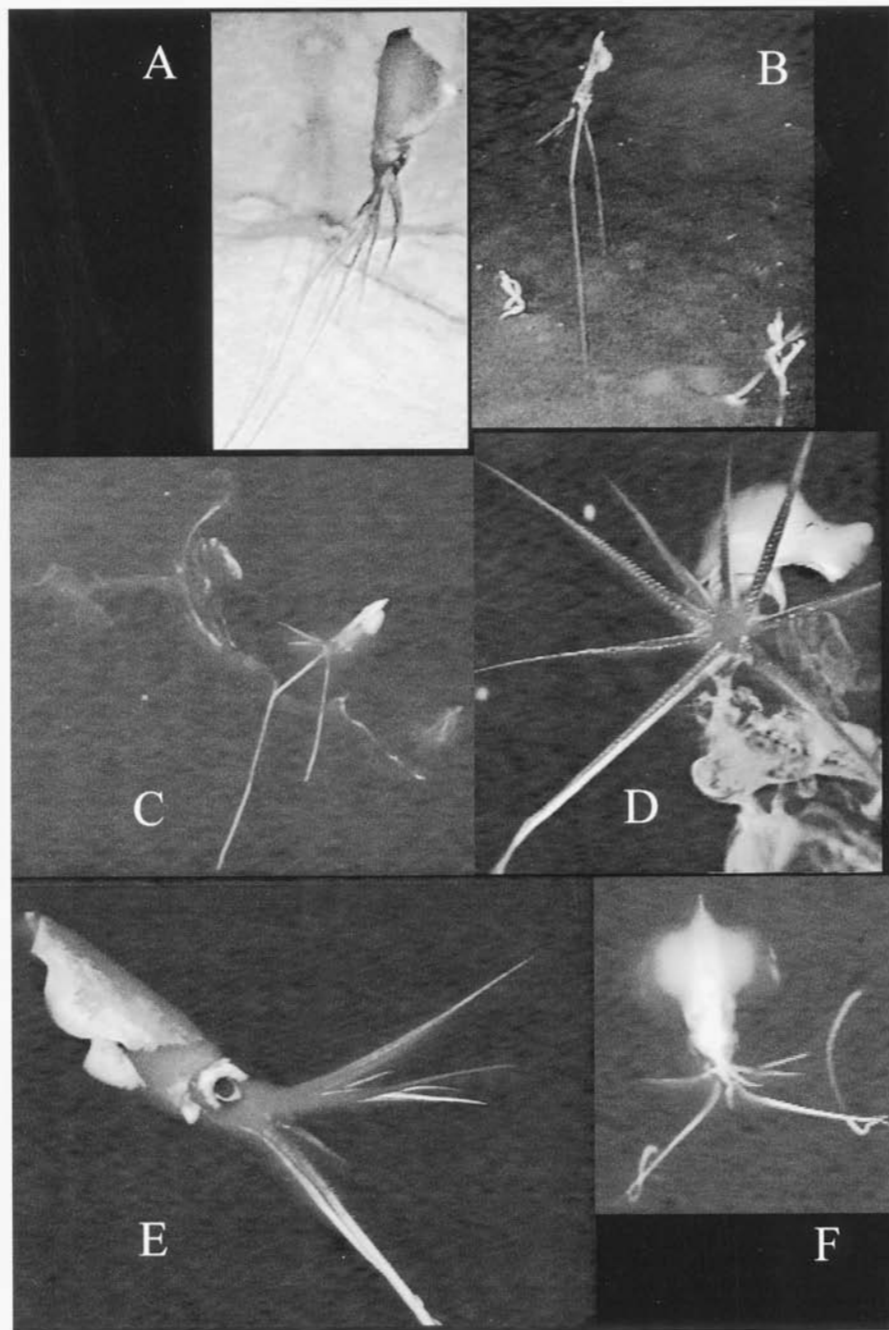
M. hjorti was observed six times on five dives for a total of 27 min recorded on videotape. It was always near the bottom (Fig. 1A,B) at depths of 600–840 m. Water temperatures were 5.5–5.7°C. Posture was very similar to that of *Mastigoteuthis magna* described by Roper and Vecchione (1997) and *Mastigoteuthis* sp. by Young et al. (1998). The head-down orientation was maintained by complex undulations (both dorso-ventral beats and postero-anterior waves) of the fins. Tentacles were held in the tentacular sheaths of the ventral arms (Fig. 1A–F).

Often, mucoidal ink was seen in the water around the squids (Fig. 1C,D). This was reminiscent of the mucus that Roper and Vecchione (1997) reported stuck to the tails and fins of several *M. magna* and to that observed on *Histioteuthis* sp. (C. Roper and M. Vecchione, pers. observ.). The ink eventually formed long, stringy shapes reminiscent of the long arms and tentacles of the squids. We have no information on whether the ink is luminescent, as it is in a number of the deep-sea species of squid.

One squid was observed gently pumping a cloud of ink into the surrounding water (Fig. 1D), in which the squid remained without swimming away. The impression created by this activity is that the squid was forming an ink cocoon in which it would remain while the mucoidal ink dissipated very slowly.

M. hjorti exhibits a surprising variety of red and white color patterns, considering that it is thought to occur at depths where color change is of little value. The animal in Figure 1E has just gone from all-red to accentuated white on the fin edges, posterolateral head, funnel and ventral arms (Fig. 1F). The squid in Figure 1E quickly transformed from all red to all white with darkened red fin edges. We want to emphasize that this color change was in the presence of the extremely bright lights of the submersible.

Figure 1. (Opposite page) *Mastigoteuthis hjorti* Chun, 1913. A. One of six observations of animals in a typical head-down orientation drifting along the bottom at 600–840 m depth; tentacles, held in tentacular sheaths of the fourth arms, trail in contact with the substrate. B. Stereotypical posture, as above, of another animal. C. Mucoidal ink, possibly a functional pseudomorph, ejected by animal in foreground; note similarity of ink morph to the animal shape and configuration. D. Animal gently ejecting ink cloud without jetting away; subsequently, ink enshrouded the animal in a cocoon-like mass. E. Color pattern assumed immediately subsequent to all-red phase; note white accents on edges of the fins, funnel, posterior head and ventral arms. F. All-white color pattern assumed following all-red pattern; note fin edges with darkened red pigmentation.



Octopoteuthis megaptera (Verrill, 1885)

Two *O. megaptera* were observed and recorded for a total of 10 min during the same dive series on which the *M. hjorti* were seen. The characteristic tail of this species can be seen clearly (Fig. 2A,B). We have depth data only for one animal, which was found a few meters above the bottom at 730 m, in water of 6.2°C. When one animal was first observed it was suspended horizontal and virtually motionless, neutrally buoyant in the water column. All arms were spread out laterally in a flat, horizontal plane and the fins were also horizontal in a rigid, extended, lateral position. In the vicinity of the submersible both squids adopted and maintained a posture in which the body was oblique with the head diagonally upward and the arms flexed dorsally and laterally (Figs. 2A–D). The posteriorly-directed arms expose the hook-bearing oral surface of the arms. The arm-tip photophores are displayed, as seen in the photograph (Fig. 2D).

O. megaptera swims by abbreviated flapping of the fins. The fin tips overlap substantially at the maximum extent of the ventral stroke, but hardly pass above the body plane on the dorsal stroke (Fig. 2A,C).

One squid (Fig. 2C,D) had damaged fins. A ragged semicircular piece of tissue was cut out of one fin (right) and a similar semicircular damaged area was outlined but not missing from the left fin. Some arm tips and photophores were missing (Fig. 2C,D).

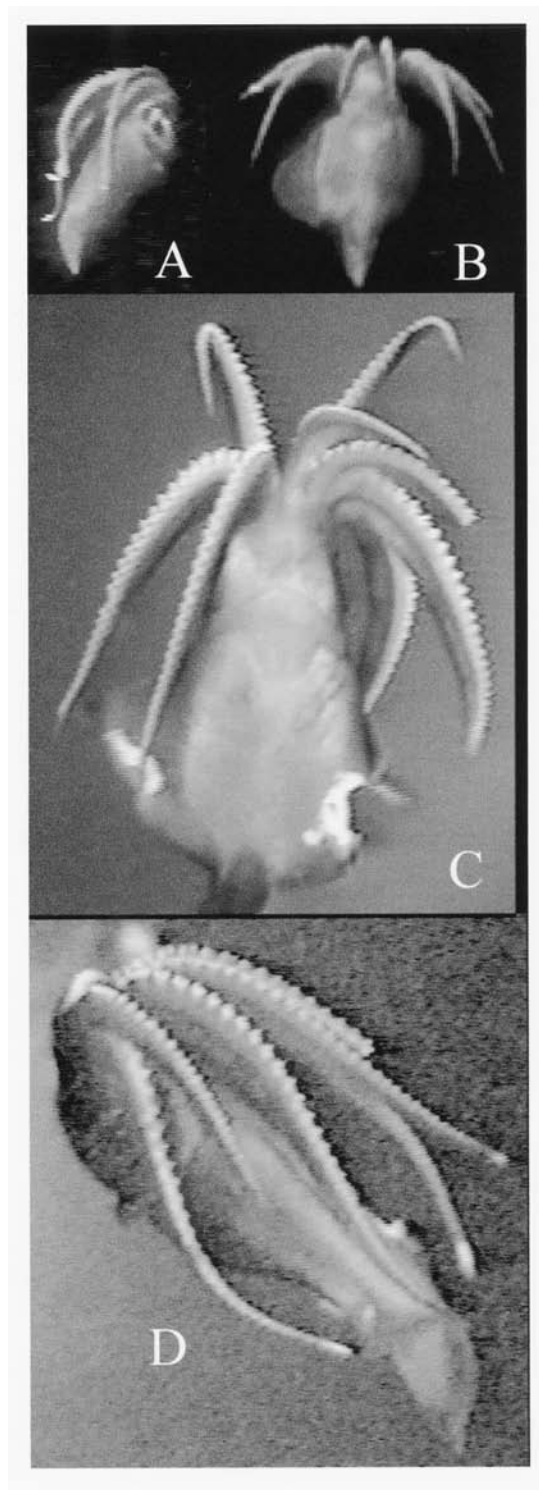
Family Magnapinnidae Vecchione and Young, 1998

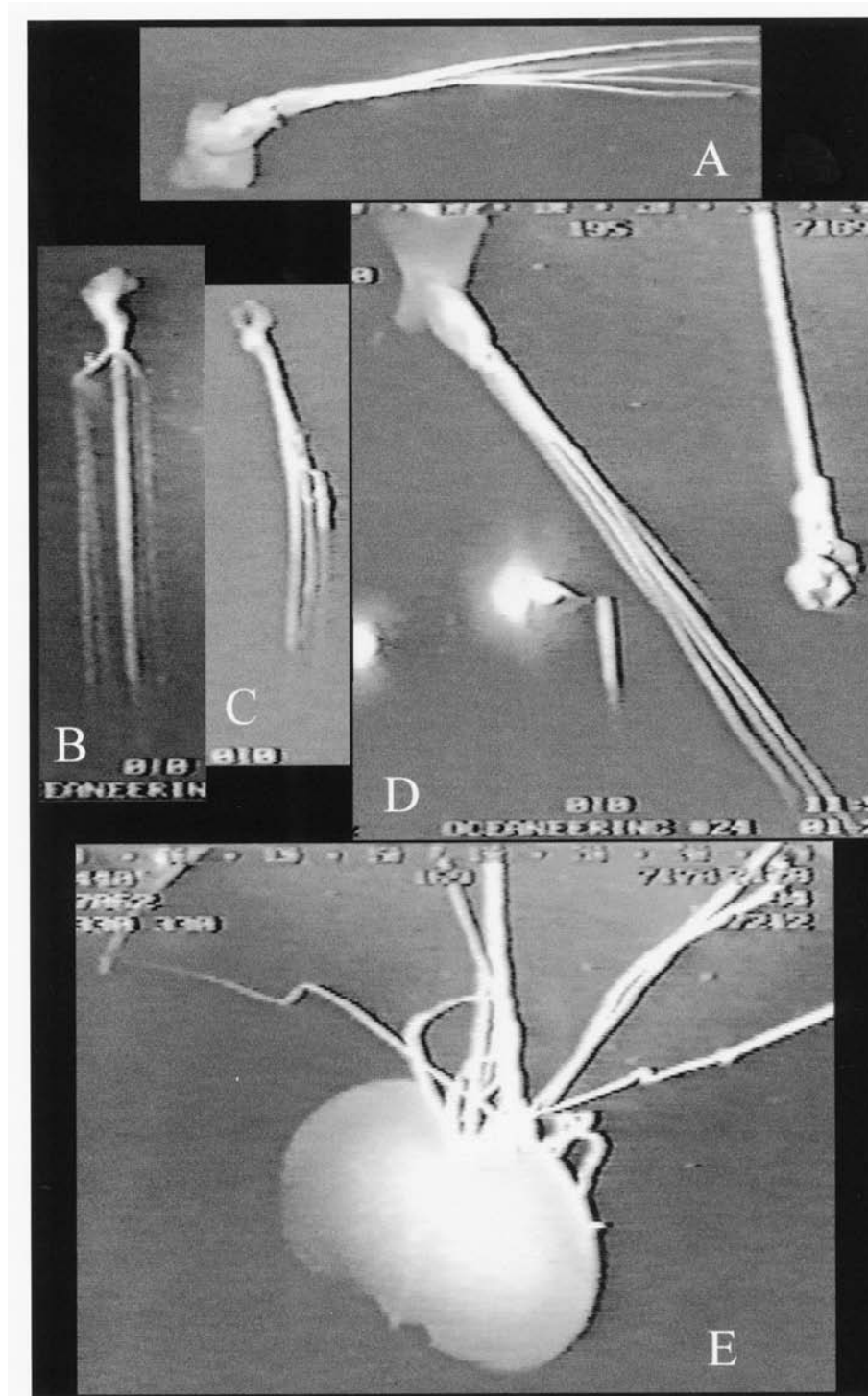
A very unusual squid was videotaped hovering near the bottom at approximately 2200 m in the northern Gulf of Mexico. When first observed from the ROV (Fig. 3B,C), this squid was in a posture very similar to that of a mastigoteuthid (e.g., *M. magna* or *M. hjorti*). The body was vertically oriented, with the head downward. This posture was maintained by complex sinusoidal undulations of the fins. However, quite unlike any known mastigoteuthid, and indeed any previously known family of cephalopods, all arms and tentacles were extraordinarily long. The arms bent and dangled straight downward from an ‘elbow’ a short distance distal to the head (Fig. 3B). Tentacles did not appear to differ in gross appearance from the arms.

After being disturbed by the ROV, the squid began to swim by strongly flapping its fins (Fig. 3C,D). When flapping, the fins overlapped dorsally to a great extent, but the tips of the fins barely touched on the ventral sweep of the stroke. No jetting independent of the fin swimming was observed from the funnel. The arms and tentacles could be retracted somewhat, but they remained very long (Fig. 3A–D) and were towed passively behind as the squid swam in the tail-first (posterior) direction.

The squid became entangled in the ROV and its tether several times (e.g., Fig. 3E). At such times it seemed to have difficulty releasing its arms and tentacles from contact with

Figure 2. (*Opposite page*) *Octopoteuthis megaptera* (Verrill, 1885). A. Lateral view of stereotypical oblique posture with head upward, arms flexed posteriorly/dorsolaterally over head; fins in ventrally folded phase of the stroke. White tips on arms are reflections from arm-tip photophores; 730 m depth. B. Dorsal view of same animal with arms flexed posteriorly and laterally; fins in lateral phase of stroke; note left arm III photophore. C. Dorsal view of second animal with arms flexed posteriorly and laterally; fins in lateral phase of stroke; note missing tissue on right fin, damaged left fin, missing arm tips. D. Dorsolateral view of same animal as Figure 2C with arms posterodorsally positioned; fins in ventral phase of stroke; note strongly exposed hooks and reflections of arm-tip photophores.





the ROV, similar to our previous observations of the tentacles of mastigoteuthids which are 'sticky' because of the extremely numerous, minute suckers. The squid would attempt to swim away and multiple appendages (arms still could not be distinguished from tentacles, even in close views) would stretch greatly. The submersible operators estimated the total length of the animal with fully stretched appendages to be approximately 7 m.

DISCUSSION

The principal in situ observations we report on three species of deep-sea squids concern orientation, locomotion and coloration. *M. hjorti* shows close similarities to *M. magna* which also occurs very close to the bottom (Roper and Vecchione, 1997). The orientation of *M. hjorti* when first encountered and undisturbed seems to confirm a stereotypical position for mastigoteuthids dwelling near the bottom (see also Young et al., 1998). The animal hangs vertically, head downward; the tips of the tentacular clubs are in contact with the bottom. The animal maintains its posture by fin undulations, while drifting slowly with the bottom currents. The impression is one of predation by trolling through the epibenthic soup of small organisms and organic material. The posture is reminiscent of a tuning fork-shape. The tentacles are enclosed in and supported by the tentacular sheaths for the length of the separated and slightly curved ventral arms, then dangle their full extent to the substrate. Stereotypical positions also have been described for other families including species of the family Cranchiidae (the 'cockatoo-position') and Histoteuthidae ('curled up') (Vecchione and Roper, 1992). Locomotion also is similar among the observed species of *Mastigoteuthis* in association with the stereotypic orientation and trolling behavior. Fin motion consists mainly of complex, sine-wave undulations, with the fins mostly in a lateral position, occasionally folding ventrally. These actions provide a head downward orientation with a steady and slow drifting along the bottom substrate.

The unusual inking behavior by *M. hjorti* observed here in detail helps to explain the mucoidal material observed on or around other deep-sea squids, e.g., *M. magna* and *Histioteuthis* sp. (Roper and Vecchione, 1997). Quite unlike the vigorous discharge of an ink pseudomorph in shallow water squids, with simultaneous rapid, jet-escape reaction, the inking behavior of *M. hjorti* is rather subdued and gentle. No jetting escape occurs, nor is the ink discharged vigorously. Instead, the squid gently expels a puffy, mucoidal cloud that enshrouds the animal in a cocoon-like mass. In fact, the funnel bends ventrally and posteriorly to distribute the ink around the body. We hypothesize that the ink cocoon functions as a chemical shield to disguise the olfactory signature of the squid from its potential predators. Alternatively, the mucoidal ink might serve as a noxious repellant to predators. Only after several minutes does the ink begin to disperse into long, appendage-like strands that could represent outstretched arms and tentacles, as a pseudomorph. This seems to be in conjunction with the remarkable change in color of the entire animal from

Figure 3. (*Opposite page*) Magnapinnidae Vecchione and Young 1998; 2200 m depth, near bottom. A. Lateral view of squid in horizontal swimming position; note large fins, extremely elongate arms and tentacles. B. Dorsal view of squid in posture upon initial encounter with ROV: head vertically downward, strongly undulating fins; note extremely long arms and tentacles (indistinguishable from each other), arms bent at 'elbows' near bases. C. Squid as it begins to swim away from disturbance of ROV, flapping fins. D. Squid swimming tail-first; note very large, strongly stroking fins, extremely elongate arms (total length of squid estimated at 7 m). E. Squid entangled in ROV; note very large fins in lateral phase of stroke, arms and tentacles stuck to ROV.

essentially all-red to all-white. Whether the ink also is luminescent, as in the case for some other deep-sea squids, cannot be determined in the video tapes. The strikingly vivid color and color pattern changes displayed by *M. hjorti* are unlike any we have observed in other deep-sea cephalopods. Many deep-sea mastigoteuthids are thought to be basically monochromatic, exhibiting a deep red to maroon coloration over the entire body with few or no chromatophores. This coloration all appears primarily to be dense ground pigmentation rather than active chromatophores. However, in *M. hjorti*, the rapid changes from solid red, with or without white accented areas, to all-white or to mostly white with accentuated red patterns on various anatomical parts, suggest previously unrecognized capabilities. How this color change is accomplished and why it would be necessary in this low-light environment remains a mystery.

O. megaptera appears to have two stereotypic positions: the horizontally flattened, motionless, neutrally buoyant posture and the obliquely oriented posture, with head upwards, arms flexed dorsally and laterally posteriorad along the head and mantle. An unusual feature of one animal was the semicircular piece of tissue missing from one fin, while the other fin had a distinct semicircular outline indicative that a flap of similarly damaged tissue. Furthermore, several arm tips were missing. We have observed similar damage on trawl-caught specimens over the years, which we attributed to rough tumbling or even pseudo-predation by other captive animals within the trawl. However, our current *in situ* observations of animals unmolested by humans indicate that the damage was the result of some form of natural damage, perhaps attacks by small predators.

The difference between *M. hjorti* and *O. megaptera* in swimming behavior with the large fins is striking. *M. hjorti* generally holds the fins within a few degrees dorsal and ventral to the horizontal plane and locomotion is achieved by complex sinoidal undulations of the fins rather than from strong flapping motions. *O. megaptera*, on the other hand, swims with such strong ventral strokes that the lateral edges of the fins overlap considerably on the down stroke. But the return stroke barely extends dorsally beyond the horizontal plane of the body.

The identity of the third species of very large-finned squid reported here is unconfirmed. However, the combination of very large terminal fins and unusual arm crown suggests the possibility that this is a magnapinnid. While the current paper was in preparation and production, Vecchione et al. (2001) published a brief note highlighting the emergent observation that this report of a probable magnapinnid is one of several from bathypelagic waters around the world. Individual reports on the details such as behavior observed during these encounters, such as the present one, are forthcoming.

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